PREDATOR-PREY CO-EVOLUTION OF *PORTIA FIMBRIATA* AND *EURYATTUS* SP., JUMPING SPIDERS FROM QUEENSLAND

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Portia is a salticid that preys on other spiders and *Euryattus* sp. is a salticid that nests inside suspended rolled-up leaves. *Portia* and *Euryattus* are sympatric at a site near Cairns but not known to be sympatric at other sites studied. *Portia* from the Cairns site practices a unique prey-specific predatory behaviour against *Euryattus*, and *Euryattus* from this site is efficient at detecting and defending itself against *Portia*. *Euryattus*, but not *Portia*, is present at a site near Davies Creek which, although only ca 15km from the Cairns site, is more xeric and at a higher elevation. Three types of tests were carried out to compare *Portia*'s efficiency at catching adult allopatric versus sympatric *Euryattus* (Test 1), allopatric *Euryattus* juveniles versus juveniles of another salticid species on which *Portia* is known to prey (Test 2) and allopatric versus sympatric *Euryattus* juveniles (Test 3). In these tests, *Portia* behaved similarly toward allopatric (Davies Creek) and sympatric (Cairns) *Euryattus*, except that it attacked and killed allopatric more often than sympatric *Euryattus*. Allopatric *Euryattus*, in contrast to Cairns *Euryattus*, appeared not to recognize an approaching *Portia* as a predator.□*Portia fimbriata*, *Euryattus*, *Jacksonoides*, *co-evolution*, *allopatry*, *sympatry*.

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Portia is a genus of specialized jumping spiders (Salticidae) that prey on other spiders (Jackson and Hallas, 1986). *Portia* is a detritus mimic and has a unique, slow, choppy style of locomotion that seems to preserve its crypsis. There are seven described species of *Portia*, distributed in the tropics of Africa, Asia, and Australasia (Wanless, 1978). A population of *Portia fimbriata* (Doleschall) in Queensland uses specialized behaviour to catch other species of salticids (Jackson and Blest, 1982). This population of *P. fimbriata* also uses a prey-specific predatory behaviour against females of a particular sympatric salticid, *Euryattus* sp. (Jackson and Wilcox, 1990).

Euryattus females suspend a dead, rolled-up leaf by strong guylines from rock ledges and tree trunks, then use the leaf as a nest (Jackson, 1985). *Portia* has never been observed to attempt to catch *Euryattus* by going inside the rolled-up leaf. However, in Queensland, *P. fimbriata* uses vibratory displays to lure *Euryattus* females from their nests (Jackson and Wilcox, 1990). These displays apparently mimic courtship displays of *Euryattus* males (Wilcox and Jackson, unpubl. data). Other species of *Portia* and populations of *P. fimbriata* in areas from which *Euryattus* is absent do not perform these displays (Jackson and Wilcox, 1990).

Queensland *P. fimbriata* will wait for hours at a time for *Euryattus* to come out of its nest (Jackson and Wilcox, 1990). Often, *Euryattus* actively defends itself by leaping at *Portia* and driving it away (Jackson and Wilcox, 1990). This is unusual behaviour for a salticid. From thousands of observations of interactions between *P. fimbriata* and many different species of salticids (Jackson and Hallas, 1986), it is evident that *Euryattus* is more efficient than other salticids at recognizing and defending itself against an approaching *Portia*. Also, in laboratory tests (Jackson and Wilcox, 1990), *Euryattus* readily recognized an approaching *Portia* as a potential predator, whereas *Jacksonoides queenslandica*, another salticid on which *P. fimbriata* feeds (Jackson and Blest, 1982), did not recognize *P. fimbriata*. This suggests an evolutionary 'arms race' (sensu Dawkins and Krebs, 1979) between *Euryattus* and *P. fimbriata*. Frequent predation by *P. fimbriata* on *Euryattus* may have favoured special abilities in *Euryattus* to recognize and defend itself against *P. fimbriata*. This, in turn, may have resulted in the evolution of refinements of *P. fimbriata*'s predatory behaviour. To test this hypothesis, we must compare the behaviour of *Euryattus* in populations with and without *Portia*. Recently, such an opportunity arose when *Euryattus* were found in an area in which *Portia* was not known.

MATERIALS AND METHODS

Cages, maintenance, terminology, basic testing procedures and analysis are given in Jackson and Wilcox (1990). Laboratory cultures of sympatric *Euryattus*, *J. queenslandica* and *P. fimbriata* were established, using spiders collected from rainforest near Cairns at about sea level (see Jackson, 1985; Jackson and Hallas, 1986). A laboratory culture of allopatric *Euryattus* was established from spiders collected in an *Acacia-Eucalyptus* woodland beside Davies Creek, near Davies Creek National Park in the Atherton Tableland (about 15km from the study site near Cairns and at c. 500m elevation). *Portia* has never been recorded from this and other Atherton Tableland habitats (Wanless, 1978; Jackson, unpubl. data). Unless noted otherwise, all spiders tested were reared in the laboratory from eggs of field-collected spiders. No individual spiders were used in more than one test. In this paper, we refer to *Euryattus* from Cairns and Davies Creek as 'sympatric *Euryattus*' and 'allopatric *Euryattus*', respectively. There were no evident differences related to general behaviour between these two populations of *Euryattus*. In particular, similar leaves were suspended by females for nests and males courted with similar vibratory displays.

The systematics of the genus *Euryattus* remains uncertain. Whether the two populations of *Euryattus* we studied are one or two different species is not now known. Voucher specimens were deposited at the Florida Collection of Arthropods (Gainesville) and the Queensland Museum.

We conducted three tests. In Test 1, *Portia* was given access to an adult allopatric *Euryattus* female in her nest. In Test 2, on alternate days, *Portia* was given access to a juvenile (2-3mm in body length) allopatric *Euryattus* and a juvenile (2-3mm) *J. queenslandica* in a bare cage (i.e., no nest or other objects present). In Test 3, on alternate days, *Portia* had access to a juvenile (2-3mm) of an allopatric and a juvenile of a sympatric *Euryattus* in a bare cage. To begin each type of test, *Portia* was placed into a cage containing the other spider shortly after lights came on in the laboratory (0800 hours). Spiders were observed continuously until predation occurred or until 4h had elapsed. Each test was either identical or at least similar to tests carried out previously (Jackson and Wilcox, 1990).

Data from Test 1 using allopatric *Euryattus* adults were compared to data from the identical type of tests using sympatric *Euryattus* adults in an earlier study (Jackson and Wilcox, 1990) to see whether *Portia*'s capture efficiency against allopatric *Euryattus* adults was greater than against sympatric *Euryattus* adults. Test 2 using allopatric *Euryattus* juveniles was compared to type 2 tests in Jackson and Wilcox (1990) using sympatric *Euryattus* juveniles and *J. queenslandica* juveniles. We already know that *Portia* captures *J. queenslandica* juveniles more efficiently than it captures sympatric *Euryattus* juveniles (Jackson and Wilcox, 1990). Here we examine whether *Portia*'s capture efficiencies against these two salticids vary when *Euryattus* is allopatric. Test 3 enabled us to compare *Portia*'s efficiency at capturing allopatric and sympatric *Euryattus* juveniles.

Adult body length is c.8mm for both *J. queenslandica* and *P. fimbriata* and for both populations of *Euryattus*. Jackson and Wilcox (1990) used three size classes, defined by the ratio of prey to predator body volume, when testing *P. fimbriata* with juvenile salticids: small (0.1-0.25), medium (0.5-1), and large (1.5-2). Only two of these (medium and large) were used here.

McNemar tests for significance of changes were used for statistical analyses of the results from Tests 2 and 3, these tests being designed as paired comparisons (Sokal and Rohlf, 1981): each individual *Portia* was used in one test with one salticid and another test with the other salticid 48 h earlier or later (decided randomly). Yates' corrections were applied to the McNemar tests, and the Bonferroni adjustment (see Rice, 1989) was made to significance levels whenever single data sets were used in multiple comparisons.

RESULTS

Test 1: *Euryattus* Adult in Nest

P. fimbriata behaved similarly toward allopatric (herein) and sympatric (Jackson and Wilcox, 1990) *Euryattus*, except that it attacked and killed allopatric *Euryattus* more frequently than sympatric *Euryattus* (Fig. 1, test of independence, $P<0.01$). Allopatric *Euryattus* appeared less prone than sympatric *Euryattus* to recognize *P. fimbriata* as a predator: 85% of the *P. fimbriata* got onto the leaf with allopatric *Euryattus*, but only 43% got onto the leaf with sympatric *Euryattus*; 23% of sympatric *Euryattus*, but only 4% of allopatric *Euryattus*, drove *P. fimbriata* away (Fig. 1).

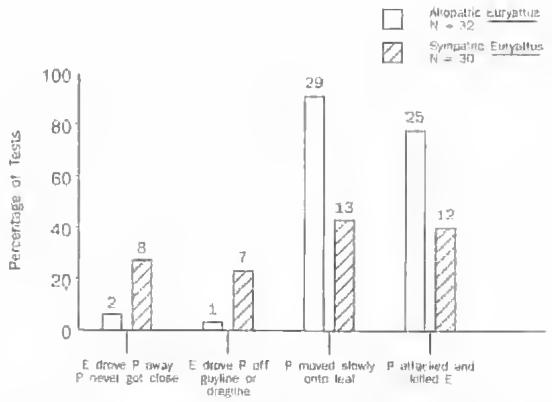

FIG. 1. *P. fimbriata* (P) tested with adult allopatric (Davies Creek) and sympatric (Crystal Caseades) *Euryattus* females (E) in suspended, rolled-up leaves. Data for sympatric *Euryattus* from Jackson and Wilcox (1990). Close: on leaf or guyline connected to leaf, or dropping on dragline toward leaf. For each outcome of test, number given above bar and percentage is read from axis.

Test 2: Juvenile *Euryattus* and *Jacksonoides queenslandica*

There was no evidence that *Portia* captured or stalked *J. queenslandica* more frequently than allopatric *Euryattus* (Figs 2, 3, McNemar tests, NS). Allopatric *Euryattus* did not appear to recognize *Portia* as a predator any more readily than did *J. queenslandica*.

Test 3: Cairns and Davies Creek *Euryattus* Juveniles

There was no evidence that *Portia* stalked sympatric *Euryattus* any more frequently than allopatric *Euryattus*, but *Portia* caught allopatric

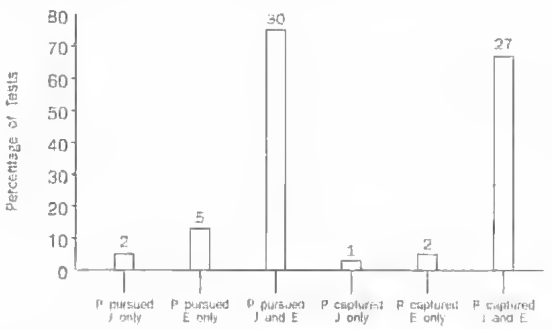

FIG. 2. Responses of *P. fimbriata* (P) to medium size (see text) allopatric *Euryattus* (E) and sympatric *J. queenslandica* (J). 40 paired tests: each *Portia* tested with one *Euryattus* and, on an alternate day, with one *Jacksonoides* (see text). Data for 'P pursued neither J nor E' and 'P captured neither J nor E' not displayed.

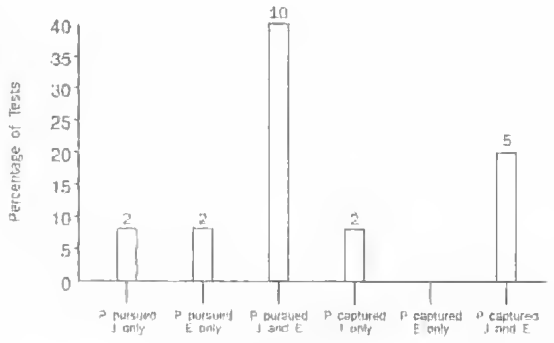

FIG. 3. Responses of *P. fimbriata* (P) tested with large (see text) allopatric *Euryattus* (E) and sympatric *J. queenslandica* (J). 25 paired tests: each *Portia* tested with one *Euryattus* and, on an alternate day, with one *Jacksonoides* (see text). Data for 'P pursued neither J nor E' and 'P captured neither J nor E' not displayed.

Euryattus more often that it caught sympatric *Euryattus* (Figs 4, 5).

DISCUSSION

Only one population of *Portia fimbriata* from Cairns studied (Jackson and Wilcox, 1990) is sympatric with *Euryattus*. *Euryattus* suspends a rolled-up leaf for a nest, and this is the only salticid sympatric with the Cairns *Portia*, or with any other *Portia* studied, known to do this. Only the Cairns *Portia* is known to use a prey-specific predatory behaviour against *Euryattus*. The sympatric (Jackson and Wilcox, 1990), but not the allopatric, *Euryattus* appears readily to recognize and defend itself against *Portia*. In fact, the al-

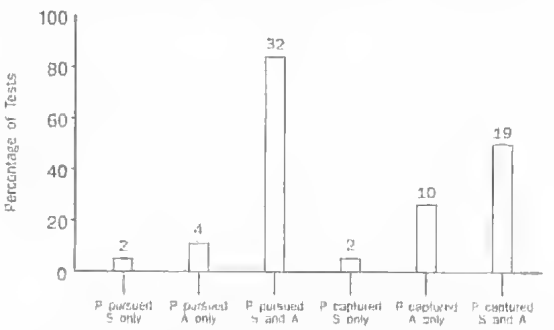

FIG. 4. Responses of *P. fimbriata* (P) to medium size (see text) sympatric (S) and allopatric (A) *Euryattus* sp. juveniles. 38 paired tests: each *Portia* tested with one sympatric and, on an alternate day, with one allopatric *Euryattus* (see text). Data for 'P pursued neither S nor A' and 'P captured neither S nor A' not displayed.

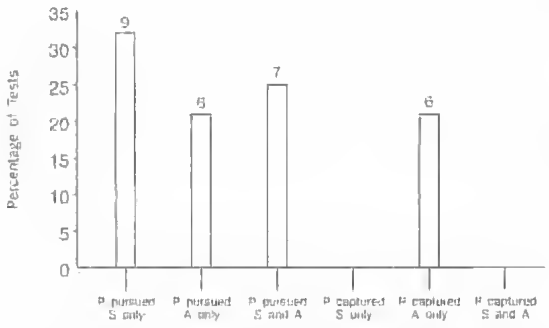

FIG. 5. Responses of *P. fimbriata* (P) to large (see text) sympatrie (S) and allopatrie (A) *Euryattus* sp. juveniles. 28 paired tests: each *Portia* tested with one sympatric and, on an alternate day, with one allopatrie *Euryattus* (see text). Data for 'P pursued neither S nor A' and 'P captured neither S nor A' not displayed.

lopatric *Euryattus* appears to be no better than *J. queenslandica* at escaping predation by *Portia* , whereas *Portia* captured *J. queenslandica* more efficiently than it captured the sympatric *Euryattus* (Jackson and Wilcox, 1990). The ability of the Cairns *Euryattus* appears to be a predator-specific antipredator behaviour.

Population differences were evident despite there being no known prior experience of the predator by the prey or the prey by the predator under laboratory rearing conditions in this and the earlier (Jackson and Wilcox, 1990) study. These findings suggest that, in the Cairns area, *Portia* and *Euryattus* appear to have acted as selective agents on the evolution of each other's behaviour.

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